OBSERVATIONS PERTINENT TO THE ROLE OF SEXUAL SELECTION IN THE STONEFLY *PTERONARCELLA BADIA* (PLECOPTERA: PTERONARCYIDAE)[1]

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ABSTRACT: Virgin males of *Pteronarcella badia* delivered semen volumes of just over one percent of their body weight. Mated females oviposited the great majority of their eggs shortly after mating and thereafter remained unreceptive to male drumming calls and tactile contacts. Implications of these findings are discussed in relation to sexual selection theory.

Much work and even more theorizing has appeared over the past two decades in the area of sexual selection. Perhaps not surprising, much of this work has involved insects (Thornhill and Alcock 1983, Alexander and Borgia 1979, Kaneshiro 1983, Carson 1978, West-Eberhard 1984, and many others). Some workers imply that sexual selection is, in varying forms and to varying degrees, essentially ubiquitous in sexually reproducing animals (West-Eberhard 1984, Thornhill and Gwynne 1986).

My work with the reproductive calling behavior of stoneflies (drumming) has led to the question of sexual selection's possible role in shaping adult behavior(s) in this interesting but inadequately studied group. This paper will deal with two aspects of reproduction which bear on the nature and degree of sexual selection pressures to be expected in stoneflies. The first question is that of semen volume transferred by males during mating. The second is the relative degree of polygyny/ployandry typical of stoneflies.

MATERIALS

Mature *Pteronarcella badia* (Hagen) nymphs were collected from the Conejos River, Conejos Co., CO in late June 1988 just before peak emergence of the adults. Nymphs were transported to the lab (Southwest Texas State University, San Marcos, TX) for rearing in chilled styrofoam ice chests. Adults were separated at emergence to insure virgin condition. Small triangular enclosures of sheet balsa wood (7.5 mm/side and 1.5 mm deep) with clear plastic lids were used to contain adults during observations. All virgin contacts, including matings, were between adults two to three days old. Pre- and post-mating weights of males were made using an American Scientific Products S/P 120 scale. Values reported below are means plus or minus sample standard deviations.

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RESULTS AND DISCUSSION

Semen Weight — Six intersexual pairings of virgin *P. badia* adults were made in order to estimate the amount of semen transferred in a first mating situation. Males were weighed just before and after mating. Prior to mating, males weighted .0431 ± .0042 gr. while postmating weight was .0426 ± .0041 gr. This amounts to only a 1.12 ± .022 percent loss in body weight. In numerous other insect groups, the male transfers large semen volumes or spermatophores (from 20 to 40 percent of the male's premating weight) which are apparently used by the females in part as a nutritional resource (reviewed by Thornhill and Alcock 1983, Gwynne 1983, Thornhill and Gwynne 1986). This nourishment may be essential for final development and formation of the female's eggs, and, when in the form of a spermatophore, may actually be eaten by the female (Gwynne 1983, Thornhill and Gwynne 1986). Movement of most spermatophore/semen nutrients into the female's eggs can require from less than 24 to over 70 hours (Gwynne 1983). Generally, females are the more choosy of the two sexes due to their larger relative investment in the offspring. In species where males deliver substantial nutrients with their semen, females might be expected to mate preferentially with males capable of donating large spermatophore/semen volumes. However, this expectation will be counterbalanced by an increase in male selectivity for "optimal" females due to the male's increased material investment in the offspring (Gwynne 1983, Thornhill and Gwynne 1986). Such "role reversal", typified by choosy males, seems unlikely in *P. badia* judging from the small weight of semen transferred, and from the short time period between mating and egg laying (see below).

Males of *P. badia* show no obvious signs of choosiness in mate selection. They typically attempt mounting virgin females, non-virgin females, and even other males. Also, in two out of eight separate interspecific pairings of *P. badia* males with *Isogenoides zionensis* Hanson females (a co-emerging species at the Conejos River), the males mounted the females and attempted copulation. Each of these two males remained mounted for over five minutes before dismounting. These observations suggest a lack of identification contact pheromones in *P. badia* as well as a lack of selectivity and discrimination by the *P. badia* males.

The six intraspecific matings were not timed, but all lasted approximately 30-45 minutes. After mating, females were gently transferred to styrofoam cups with screen lids. Each cup contained three cm of river water for oviposition. All six females laid eggs shortly after mating (395 ± 54 eggs). This egg data compared favorably with that from 16 other *P. badia* females (354 ± 74 eggs) which were mated in the course of other experiments. Seven of the latter were observed to lay second clutches of eggs (55.1 ± 23.4 eggs) 2-5 days after the initial batches were laid. Two of these seven females were remated by virgin males prior to their second laying, but the other five had no secondary male contacts. These data suggest that females require only one mating for the fertilization of most, if not all, of their eggs, most of which are laid in the first oviposition event. The six females mated in the semen weight experiments lived for 11.4 ± 0.9 days.

Mated Female Response to Male Calls — Five *P. badia* males were seen to resume calling within minutes after their first mating, and two similar observations were made after second matings. Males of *Taeniopteryx nivalis* (Fitch) have also been observed to resume calling just after mating (Stewart and Zeigler 1984). These observations indicate that male stoneflies are polygynous, though to what extent is still an unanswered question. Mated female stoneflies have not been observed to answer male calls (Rupprecht 1967, Stewart and Zeigler 1984), but this observation has often been based on a female's exposure to male calls only minutes or hours after mating. To test the hypothesis that females might again become responsive to male calls after egglaying and/or some refractory period, mated females (which laid eggs within 6 hours after mating) were exposed to male calls as follows. Five females were exposed to male calls (her chamber acoustically coupled to a chamber containing a signaling male) 24 hours after mating, six females were exposed to calls 48 hours after mating, and seven females were exposed to calls 96 hours after mating. In none of these 18 exposures was a mated female observed to answer male calls. Similar acoustically coupled chambers, with the male and female in two separate but coupled chambers, have been used in previous studies to record the drumming signals of virgin stonefly pairs and have a "proven" track record of providing efficient signal transfer between the sexes (Stewart and Zeigler 1984, Zeigler and Stewart 1985).

Observations of tactile contacts between other mated females and virgin males also indicate an unwilling or at least "disinterested attitude" on the part of the females. One mated female (56 hrs post-mating) ran from a virgin male on initial contact and would probably have escaped from him in nature. As both were contained in a common chamber, the male eventually mounted her and mated. This female continued to move about the chamber while the male was engaged (virgin females typically remain motionless during the mating process). Another female, minutes after mating but before egglaying, successfully rejected a second male's mounting attempts by raising her abdomen at about a 90 degree angle from her body axis and wagging it laterally during mounting attempts.

Similar rejection responses have been noted in other stoneflies (Rupprecht 1967, Zeigler and Stewart 1977, Stewart and Zeigler 1984).

In terms of sexual selection theory, a female who puts all her eggs in one basket (fertilizes all her eggs with sperm from one male) should profit by being choosy as to which male fertilizes her eggs (Thornhill and Gwynne 1986). This is especially so for insects such as stoneflies where the male contributes nothing to the female or offspring except sperm (Borgia 1981). But, if adults are short-lived and females typically encounter males infrequently, mating with the first male encountered may be the optimal strategy due to the costs of locating two or more males and making a comparison (Wittenberger 1983). Predation, bad weather, or other environmental hazards could also make waiting around for a second more "attractive" or fit male a suboptimal strategy (Borgia 1979, Wittenberger 1983). Alternately or concurrently, if males are typically of equal or near-equal fitness and meet some minimum threshold specifications (a proposition I am now addressing in an unfinished manuscript), the female would on average, be best served by mating with the first male encountered (Wittenberger 1983). Based on years of drumming studies, I can state qualitatively that as a group virgin stonefly females are not obviously coy or choosy in selecting a mate. Females typically answer the drumming call of, and mate with, the first male encountered (these statements derive largely from laboratory observations).

In nature, females may feed and so fuel the continued development of a second large egg batch, but several hours of observations along the Conejos River during peak emergence have not yielded evidence of adult feeding (Ed Dewalt, personal communication). The data on feeding in adult stoneflies as reviewed by Hitchcock (1974) and Hynes (1976) indicate that adults of the family Pteronarcyidae, which includes *Pteronarcella*, do not feed but do drink water (and may take in honeydew or nectar). Adults of both sexes were provided with water and were seen drinking during the course of observations. In some other families, adults do feed, and in some genera the females apparently require food in order to fuel initial egg development and maturation, which can take many days (Hynes 1976), but this is obviously not the pattern in *P. badia*. Two of the 16 *P. badia* females mentioned above were mated within two hours of emergence and went on to lay a typical clutch of eggs within five hours of mating.

In conclusion, it appears likely that females of *P. badia* rely on single matings to fertilize most, if not all, of their eggs. The possibilty exists that second matings may occur shortly after the initial mating but prior to egg laying, possibly with sperm displacement by the second male, but the non-responsiveness of mated females to male calls and observations of male rejections by recently mated females argue against this being a typical event.

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